THE PARAGASTROPODA: A PROPOSAL FOR A NEW CLASS
OF PALEOZOIC MOLLUSCA

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ABSTRACT

A functional analysis of the shells of the hyperstrophic and other apparently left-handed "gastropods" of the Paleozoic suggests that these are not the shells of torted mollusks. They should not, therefore, be considered gastropods, and as they do not fall within even a broad concept of Monoplacophora we suggest that they be considered members of a new class of mollusks. This group includes the following taxa which have previously been placed in the class Gastropoda: Onychochilidae, Macluritidae, Pelagiellidae, Clisospiridae and possibly the Euomphalacea. The following new taxa are proposed: class—Paragastropoda: orders—Orthostrophina, Hyperstrophina; family—Aldanellidae.

INTRODUCTION

Among living univalve mollusks, only members of the class Gastropoda have anisostrophically coiled shells. Thus it has been presumed that all anisostrophic shells in the geologic record must, perforce, be gastropods. In 1952, on considering the shells of the Lower Cambrian genus *Pelagiella*, that astute observer of Paleozoic Gastropoda, J. Brookes Knight (Knight, 1952: 43) wrote: "I . . . [doubt] . . . that they are gastropods." However, he was not able to verbalize just what was "ungastropod" about these enigmatic shells. Recent attempts (Linsley, 1977) to reconstruct the Lower Paleozoic genus *Onychochilus* as a gastropod resulted in a rather strange looking beast (Fig. 1) and provided insight into how *Onychochilus* and *Pelagiella* differ in their appearance from typical gastropods that can be studied today.

One of the most obvious ways that *Pelagiella* and *Onychochilus* differ from modern gastropods is in the shape of the aperture. In both genera the aperture is elongated but the long axis of the aperture is oriented at approximately right angles to elongated apertures of modern gastropods. In making the reconstruction of *Onychochilus,* Linsley ended up with an organism whose shell was oriented in such a way that the long axis of the aperture was almost at right angles to the long axis of the foot. Yet according to a more recent study (McNair *et al.,* 1981) almost all modern gastropods orient their shell so that

the long axis of the aperture is subparallel to the long axis of the foot. Obviously with any given shell the head of the mollusk could be interpreted as being at either end of the aperture. In the case of *Onychochilus* if the head was at the basal end of the aperture, the organism would be interpreted as a left-handed, orthostrophic gastropod. If, however, the head of *Onychochilus* was located at the spire end of the aperture, the organism would be right-handed, hyperstrophic but untorted (Fig. 2).

It is the purpose of this paper to demonstrate that this interpretation of the shells of many Paleozoic molluscs is sound and in fact makes comprehensible many previously unexplained aspects of these shells.

TORSION IN THE GASTROPODA

Gastropods, by definition, are mollusks which have undergone torsion or are descended from torted ancestors. Torsion is a rather unusual process which results in rotation of the shell and its contained viscera 90° to 180° relative to the foot and head of the gastropod. Mechanically, torsion is a relatively simple process in that only one of a pair (primitively) of velar retractor muscles begins to function and this unbalanced pull results in rotation of the shell (Knight, 1952; Eales, 1950; Crofts, 1937; Smith, 1935). The functional significance of this process has been

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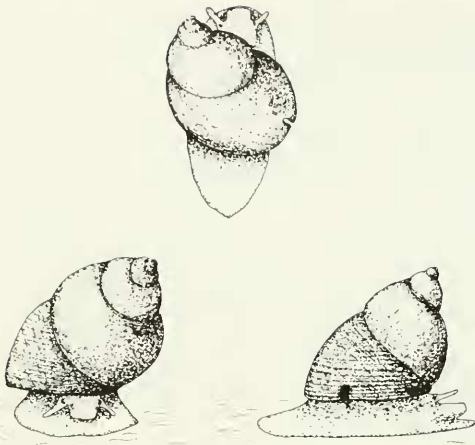[2]Department of Zoology, Duke University, Durham, NC 27706, U.S.A.

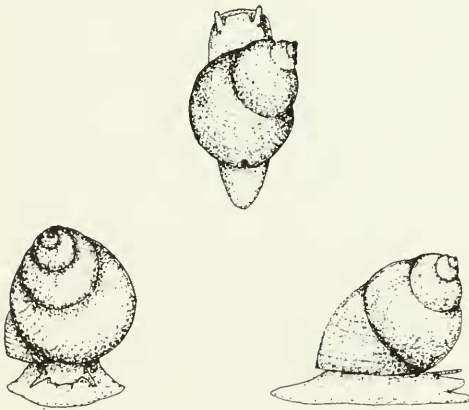FIG. 1. Reconstruction of *Onychochilus* as a gastropod (Linsley, 1977).

FIG. 2. Reconstruction of *Onychochilus* as a paragastropod.

the subject of much discussion (Ghiselin, 1966; Batten, Rollins & Gould, 1966; Runnegar & Pojeta, 1974; Thompson, 1967; Linsley, 1978a) and there seem to accrue advantages for both the larva and the adult. The immediate advantages are the result of the mantle cavity being brought over the head. This allows the larva to retract the velum into the mantle cavity (Garstang, 1928) and the adult to more effectively clamp the shell over the head region. Subsequent advantages for the adult result from the fact that once the mantle cavity is situated anteriorly it is possible to envelop a larger, more complex head and improved circulation patterns (Linsley, 1978a).

It is frequently suggested (e.g. Eales, 1950) that torsion is the cause of asymmetry of gastropods. We believe that this is an unwarranted assumption. The process of torsion and anisostrophic coiling are completely separate events, with no causal connection between them. For example, it has been argued (Knight, 1952; Horný, 1963; Yochelson, 1967; Rollins & Batten, 1968; Peel, 1974; Linsley, 1978a) that the bellerophonts are symmetrical, yet torted gastropods. Further, the monoplacophoran *Cyrtonella* has marked asymmetry. We suggest in this paper that there are numerous asymmetrical untorted mollusks. We will attempt to show that there are problems that attend isostrophic shells of more than one volution and that anisostrophism is a possible solution to this problem in both torted and untorted molluscs.

The great majority of modern gastropods are right-handed (dextral) although left-handed (sinistral) shells are fairly common. Classically, if a shell is held with the spire up and the aperture facing the observer, then the aperture will be on the right in a dextral shell and on the left in a sinistral shell. In right-handed shells the right gill is frequently lost and the anus migrates in the direction of the lost gill or towards the upper suture. Other organs, which are primitively paired, also tend to lose one of the pair during evolution. Left-handed gastropods are mirror images of right-handed gastropods, both internally and externally. Thus in a left-handed gastropod it would be the left gill that is lost. However, there also exist species that have the soft anatomy of a right-handed gastropod in an apparently left-handed shell. In these forms the anus appears to migrate away from the apex of the shell rather than towards the spire. Because of this we tend to illustrate these hyperstrophic shells with their aperture on the right as we would a right-handed shell. This has the consequence of placing the spire in a "down" position, and hence the descriptive term, "depressed spire," is used in reference to hyperstrophic shells.

It might make understanding sinistrality and dextrality of Gastropoda easier if we defined these terms relative to the process of torsion itself. Dextral gastropods are defined as those whose left velar retractor muscle aborted (or delayed development) thus causing the right retractor muscle to produce torsion so that the shell turned in a counter-clockwise manner relative to the foot as viewed from above. In sinistral gastropods it is the left retractor that

produces torsion and the shell swings in a clockwise fashion. This definition would allow us to talk about right and left-handed limpets and bellerophonts although we cannot think why anyone should. Perhaps asymmetry of the deep retractor muscles of the bellerophonts would allow us to refer to them in this way.

Recognition of hyperstrophic, orthostrophic, dextral, sinistral, torted and untorted conditions is fairly straightforward with an organism with soft parts. Then it is possible to compare the positions of internal anatomical features relative to shell geometry. However, recognition of these conditions in the fossil record is a different story. Dextrality and sinistrality (and hence orthostrophy and hyperstrophy) can be recognized by the "rule of opercula" (Cox in Knight *et al.*, 1960: I125). In dextral gastropods the operculum, if spiral, always grows in a counterclockwise direction when viewing the exposed side of the operculum. Thus the accreting margin is placed against the parietal wall of the aperture when the animal is retracted. Conversely in sinistral forms, growth of the operculum is always clockwise.

Recognition of torsion in fossils is an even more difficult problem. Because of the "bellerophont problem" all of our attention has focused on the recognition of torsion in isostrophic forms. This problem is treated in existing literature (Rollins & Batten, 1968; Linsley, 1978a) and since it is not directly pertinent to the present problem, we will not review it here. The recognition of torsion in anisostrophic shells has never been considered because of the unwarranted assumption that anisostrophy is a necessary consequence of torsion. Thus it has always been assumed that with the exception of *Cyrtonella*, all anisostrophic "gastropod" shells were necessarily torted. Obviously, some mollusk shells, such as those of turriliticone cephalopods are anisostrophic without being torted. Almost equally obviously, not all coiled shells are those of mollusks, some foraminifera and serpulid worms being examples.

## THE RULE OF APERTURAL ELONGATION AND ITS APPLICATION TO ORTHOSTROPHY AND HYPERSTROPHY

Linsley (1977) has demonstrated that gastropods support their shells over their backs so that the shell is balanced. McNair *et al.* (1981) have demonstrated that in gastropods with elongate apertures (major axis greater than 20% of minor axis), the shell is oriented with the major axis subparallel to the long axis of the foot or the antero-posterior axis of the organism. If these two generalizations are valid, they provide a possible means of recognizing torsion in a fossil, anisostrophic mollusk.

In right-handed, orthostrophic torted mollusks (the majority of modern gastropods) the spire of the shell projects to the right side of the animal and is swung towards the posterior by regulatory detorsion (Fig. 3). If a gill is eliminated, it is always the right gill and the anus migrates to the spire side of the aperture or the functional posterior portion of the aperture. Reasoning by homology, an untorted, right-handed, orthostrophic mollusk would have the spire protruding to the left side of its body and would balance the shell by swinging the spire backwards (Fig. 4), though in this instance it would be called "regulatory torsion" rather than "regulatory detorsion." If a gill were lost, it would be the left gill (which would become the right gill if torsion were to occur) and the anus would migrate to the spire side of the aperture or the functional posterior. The concept of "orthostrophy" in untorted molluscs is thus defined by homology with torted orthostrophs. Functionally, water currents will enter the base of the aperture and exit at or near the suture in orthostrophic mollusks.

In torted hyperstrophic mollusks the spire projects to the left side of the animal. Regulatory detorsion presumably swings the spire over the head of the animal (Fig. 3), but it is the right gill that is lost and the anus migrates abapically to the "base" of the aperture, which is now functionally posterior. By homology, in untorted hyperstrophic mollusks the spire projects to the right side of the organism and is swung forward over the head by regulatory torsion (Fig. 4). Elimination of the left gill (the torsional right gill) allows the anus to migrate abapically which is again functionally posterior. Again, "hyperstrophy" in untorted mollusks is defined by homology with their torted counterparts. Functionally, water currents in hyperstrophs will enter at or near the sutural portion of the aperture and exit at the base of the aperture in both torted and untorted forms. As a result of the shell balancing process, the long axis of the aperture of torted anisostrophic mollusks will be at right angles to the long axis of their counterparts in un-

HYPERSTROPHIC GASTROPODS (TORTED)
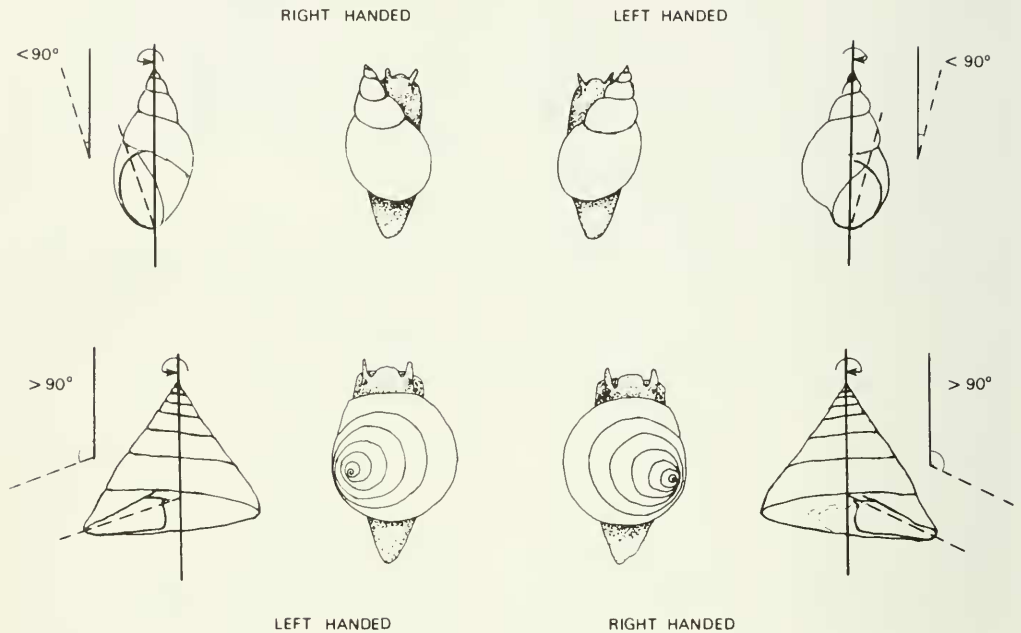
ORTHOSTROPHIC GASTROPODS (TORTED)

FIG. 3. The shell balancing process in gastropods places the spire of the shell to the posterior in orthostrophic forms and to the anterior in hyperstrophic forms. In all cases the gill and inhalant currents will be anteriorly positioned while the anus and exhalant currents will be posteriorly positioned. Since the aperture elongates sub-parallel to the long axis of the foot the two lines formed by the axis of coiling and the long axis of the aperture will form an acute angle in hyperstrophic forms and an obtuse angle in orthostrophic forms.

torted anisostrophic mollusks. Thus hyperstrophic untorted shells will tend to resemble orthostrophic torted shells in terms of apertural elongation and orthostrophic untorted shells will have apertures that elongate like those of hyperstrophic torted shells (Figs. 3 and 4).

The preceding analysis is made on the assumption that there will be direct homology between torted and untorted forms. The abundance of living prosobranch gastropods support the model of right and left-handed orthostrophic torted forms. For hyperstrophic forms our sources of confirmation are restricted indeed. Among the living hyperstrophic forms are *Lanistes* (right-handed) and *Carinifex (Carinifex) newberryi* Lea (left-handed). We have only had the opportunity to observe a single specimen of *Lanistes* in motion. When that *Lanistes* moved ahead in a straight line, the axis of coiling of its shell was only slightly inclined to the substrate and roughly at right angles to the long axis of its foot. One other "living" hyperstrophic form is a single live-collected shell of the prosobranch *Heliacus* described by Robertson & Merrill (1963). *Heliacus* normally has a hyperstrophic larva which reverts to orthostrophy in the adult. The one individual reported by them continued larval hyperstrophy into adulthood. Robertson & Merrill (1963) inferred that the anus of this form was indeed at the base of the shell and that inhalant currents entered the aperture near the suture. Thus the spire of this animal projected in front of the head, consistent with our model. It should be noted that the form of this aberrant *Heliacus* is that of a shell dragger, snails whose center of gravity is so far displaced from the aperture that they cannot support their shell over their back. Shell draggers are particularly oblivious to the relative position of their shell to their

HYPERSTROPHIC PARAGASTROPODS (UNTORTED)

RIGHT HANDED   LEFT HANDED

LEFT HANDED   RIGHT HANDED
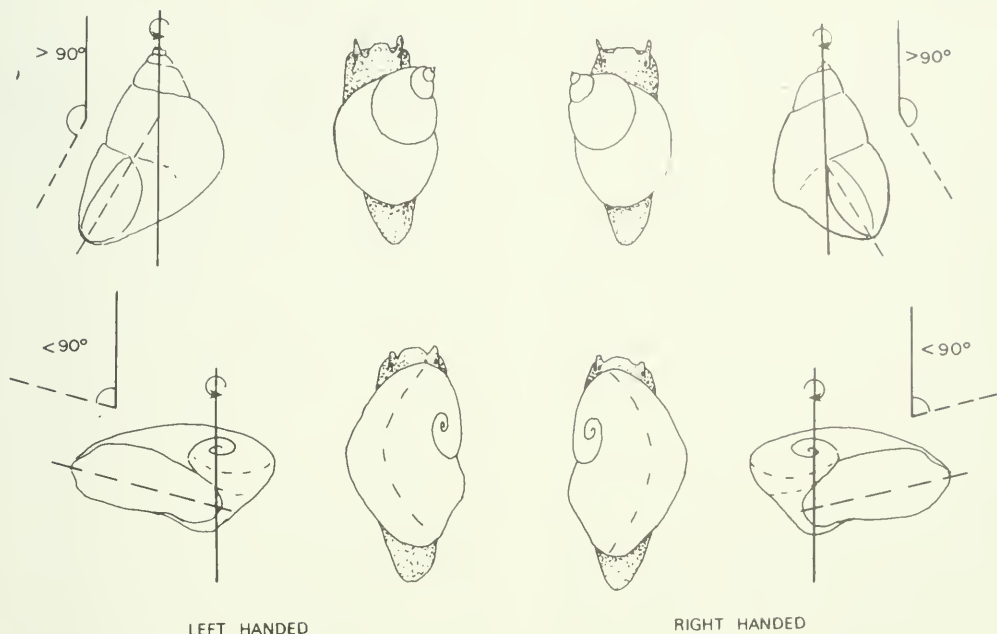
ORTHOSTROPHIC PARAGASTROPODS (UNTORTED)

FIG. 4. The shell balancing process in paragastropods places the spire of the shell to the posterior in orthostrophic forms and to the anterior in hyperstrophic forms. The gill and inhalant currents are presumed to be anteriorly placed in all instances while the anus and exhalant currents are situated posteriorly. Again the long axis of the aperture is subparallel to the long axis of the foot with the result that an acute angle will be found between the long axis of the aperture and the axis of coiling in orthostrophic forms, but it will be an obtuse angle in hyperstrophic forms.

body, seemingly as comfortable with the shell being pushed in front of them or stuck straight out to the side as they are holding it in the normal straight back position (Linsley, 1977). And since *Heliacus* is near sessile because of its mucous thread (Robertson & Merrill, 1963) it was apparently not too distressed by the abnormality and managed to survive until adulthood. Thus it can be seen that a few examples from the living world are consistent with the rule of apertural elongation, but lack of variety does not allow the living world to be very supportive.

The rule of apertural elongation cannot be applied indiscriminately. For example, the rule cannot be invoked for forms with essentially round apertures (when the long axis is less than 1.2 times the minor axis). In addition, the rule cannot be applied in cases where balancing is accomplished by regula-

tory detorsion (or regulatory torsion in untorted forms) that approaches 90°. As the axis approaches 90°, torted and untorted forms tend to converge and resemble each other. Finally, the rule cannot be invoked for sessile forms, forms with radial apertures, or any forms that do not balance their shell during locomotion.

THE PALEONTOLOGICAL RECORD

There are many fossil shells that seem to possess the shapes of untorted mollusks. These groups that we can identify with certainty include the Pelagiellidae, and the Onychochilidae. There are also other groups that we believe are untorted, but since they either have circular apertures or radial apertures we cannot be certain. These include the

enigmatic lower Cambrian genus *Aldanella*, the Macluritacea and the Euomphalacea.

Of all of these above-mentioned groups, the Onychochilidae, including *Onychochilus* Lindström and its relatives *Matherella* Walcott, *Matherellina* Kobayashi, *Laeogyra* Perner, *Sinistracirsa* Cossmann, *Kobayashiella* Endo, *Pervertina* Horný, *Invertospira* Horný, *Helicotis* Koken, and *Hyperstrophema* Horný, constitute the largest and best-known group because of the relatively well-preserved shells of various of these genera.

The onychochilids possess a number of features that seem very unusual for gastropods, but that are consistent with an interpretation of them as untorted organisms. First, all appear to be left-handed, and have been long interpreted as being hyperstrophic, a position with which we concur. However, the evidence for this is circumstantial, for no opercula have ever been found associated with any of these genera. The interpretation of this group as hyperstrophic rests on their presumed relationship with the Macluritacea which are known to be hyperstrophic because of evidence from opercula associated with their shells. The basis of the relationship of the macluritids and onychochilids rests on the fact that: 1) these are the only apparent "sinistral" forms in a Lower Paleozoic world comprised otherwise only of right-handed forms; 2) apertural shapes are quite similar (and both strangely distinct from known gastropods); 3) both have a distinctive umbilicus which is unusual when compared to most gastropods; and 4) both groups have an angulation in their apertural form which has been interpreted (Knight, 1952) as marking the position of the anus. We agree that these similarities are sufficient to establish the relationship between these two groups and thus warrants the interpretation of the onychochilids as being hyperstrophic.

In addition to being hyperstrophic, all onychochilids have prosoclinal growth lines inclined at an unusually steep angle. From this we infer that during locomotion the axis of coiling was steeply inclined to the substrate (Fig. 2). Within living gasropods the low-spired trochids have comparably steep prosocline apertures. In onychochilids we find this feature in varied geometries from the low-spired *Kobayashiella* (where it is more or less expected) to the very high-spired *Sinistracirsa* and *Matherella* where it is most unlike modern gastropods. We feel that this high angle of inclination is a necessary adaptation to hyperstrophy. Since the inhalant currents come into the aperture anteriorly and the spire is projected anteriorly, the spire of the shell has to be lifted high off the substrate to accommodate these currents.

The strangely-shaped umbilicus, unusually deep and wide when compared to gastropods of a similar geometry, can also be interpreted as an accommodation to the inhalant current. In modern gastropods the base of the shell is functionally the anterior in the majority of mobile forms, hence an open umbilicus is a source of turbulence and is rarely found in modern mobile snails. The only living gastropods with wide, open umbilici are relatively immobile ones or those who hold their coiling axis with a high inclination so that the umbilicus is functionally in a ventral position and is hidden against the upper surface of the cephalopedal mass. The base of the shell, including the umbilical area, is occasionally sculpted to accommodate a large calcareous operculum which essentially locks into place. In the onychochilids the umbilicus is functionally ventral in the living animal and occupies a position in front of the aperture. Thus a broad open umbilicus would open up this area of the shell to the anteriorly directed inhalant current, which would presumably enter near the suture.

The final unusual feature of the onychochilids which is made explicable by the interpretation of them as untorted hyperstrophs is the strangely-shaped aperture. In many onychochilids it is banana-shaped with the inner lip (which forms the umbilicus) bending abaxially to constrict the aperture on the columellar side. The aperture is generally extended or angulated at its posterior end which is interpreted as marking the position of the anus. The holotype of *Onychochilus physa* Cossmann, which is one of the best preserved specimens of the family, shows a re-entrant at the posterior portion of the lip. If this re-entrant is not an artifact of preservation, then this was strictly a feature of the adult shell, for it generates no selenizone. We do not think that it is an artifact, for there is a raised and reinforcing deposit of shell material around the re-entrant. We feel quite certain that this is an anal re-entrant which in the reconstructed living organism would be positioned in the posterior-most position, a convenient place to have an anus.

The second group that we feel certain is untorted is the Cambrian family Pelagiellidae. We interpret these shells as belonging to

right-handed orthostrophic untorted mollusks (Fig. 4, orthostrophic). In the type-species, *Pelagiella atlantoides* Matthews, the aperture is elongated at almost right angles to the coiling axis of these shells and as Knight noted (1952: 43), "I . . . [doubt] . . . that they are gastropods." Many pelagiellids have two sinuses in the aperture. One of these is typically positioned at or just above the shell periphery, as in *Cambretina mareki* Horný. In our reconstruction of this organism this sinus is in a posterior position and is interpreted as an anal re-entrant which sometimes generates a selenizone. The other re-entrant is typically located on the abapical portion of the shell and is here interpreted as the inhalant re-entrant, since it would be positioned anteriorly in our reconstruction.

We have not seen any muscle scars associated with these shells, but would expect them to be multiple and are likely to be asymmetrical due to the anisostrophism.

Another genus which deserves comment along with *Pelagiella* is the Lower to Middle Cambrian genus *Aldanella*. It is quite possible that these shells are not molluscan at all (Yochelson, 1978), but if they are, we suspect that they are shells of an untorted mollusk. Unfortunately, this can be no more than a suspicion for the apertures are not preserved, nor are growth lines from which apertural form could be deduced. At the moment of writing it is not even known if *Aldanella* has a radial or tangential aperture. If it is a radial aperture, then we would certainly agree with Yochelson that these are not molluscan. If they possess a tangential aperture, we feel it would greatly increase the probability of a molluscan affinity, for a tangential aperture implies a dorsal shell. If *Aldanella* should prove to have molluscan affinities, we would suspect an untorted condition but cannot demonstrate it at this moment because *Aldanella* has a circular whorl cross-section and we cannot invoke the rule of apertural elongation to demonstrate torsion or non-torsion.

The next group of possibly untorted mollusks is the Macluritidae, including the genera *Maclurites* Lesueur, *Palliseria* Wilson, *Scaevogyra* Whitfield, *Macluritella* Kirk, *Antispira* Perner, *Teiichispira* Yochelson & Jones, and *Versispira* Perner. The genus *Lecanospira* Ulrich & Bridge may be a macluritid, but we are more inclined to believe that they are euomphalids. All members of this group have radial apertures and are presumed to lie with one side of their shell on the substrate (Lins-

ley, 1978b). Thus the rule of apertural elongation cannot be invoked for this group. However, as mentioned above, other characters such as hyperstrophy, unusual umbilicus and general aperture shape, allow the establishment of affinities with the Onychochilidae and thus attest to the untorted nature of this group.

The Euomphalacea present a more difficult problem. There are strong similarities between the Macluritidae and the Euomphalacea, in that both groups have essentially a discoidal whorl form and a radial aperture, frequently with the suggestion of a sinus (presumably exhalant) on the "uppermost" surface of the whorl. However, it is possible that these are the result of convergence with two groups independently adapting to the sedentary suspension-feeding niche. Since the euomphalaceans have circular whorl profiles *and* radial apertures, it is impossible to invoke the rule of apertural elongation to infer the condition of torsion. However, we suspect that the similarities between these two groups are not those of convergence but of common descent and would suggest that they may indeed be untorted.

The final group to be considered as a possible candidate for untorted, anisostrophic mollusks is the Clisospiridae, including the genera *Clisospira* Billings, *Mimospira* Koken, *Ferrogyra* Horný, *Conoclisa* Horný, *Trochoclisa* Horný, *Antigyra* Horný, *Antizyga* Horný, *Atracura* Horný, *Bodospira* Wängberg-Eriksson, *Angulospira* Wängberg-Eriksson, *Tapinogyra* Wängberg-Eriksson, and *Undospira* Wängberg-Eriksson. This is a poorly known group, but Upper Ordovician specimens recently described from Sweden (Wängberg-Eriksson, 1979) strongly suggest that they are closely related to the Onychochilidae and should be considered untorted. They are all hyperstrophic and have the same elongated aperture and broad umbilicus as have the Onychochilidae. Horný (1964) noted the similarities between the Clisopiridae and the Onychochilidae and recommended that both be subsumed under the Onychochilidae.

PHYLOGENY

We suspect that the Paragastropoda are polyphyletic and that the orthostrophic pelagiellids are not related to the hyperstrophic onychochilids. Thus we look upon the class

Paragastropoda as being a grade of organization rather than a clade.

Anisostrophy is regarded as a solution to the problems attendant to isostrophic coiling rather than torsion. If a mollusk with a dorsally situated shell develops an isostrophically coiled shell with the spire placed over the head of the organism, then this coiled mass and the body stalk of the animal will effectively block inhalant currents from the anterior position (Linsley, 1978a). As a result, cyclomyan monoplacophorans of more than one volution all show the development of angulations of the lateral apertural margins to accommodate laterally placed inhalant currents. Torsion was one solution to this problem for it eventually allowed the inhalant currents to move anteriorly into the now forward-placed mantle cavity (Linsley, 1978a). But even after torsion had produced the bellerophontids, however, anisostrophy eventually produced an even better solution by placing the left gill in a more anterior and more favorable position. The Paragastropoda provide a second solution to the problem of the laterally displaced inhalant currents. The development of anisostrophy causes a repositioning of the shell through the shell balancing process. Either orthostrophy or hyperstrophy serves to place the pretorsional right gill in an anterior position. The fact that both *Pelagiella* and *Onychochilus* have elongated apertures strongly suggests that both have lost the left gill.

It is obvious that once this adaptation had occurred, these animals must have been an evolutionary dead end. They could not serve as ancestors to the gastropods because torsion would serve to place the anus in front of the gill and necessitate a complete reordering of water current through the mantle cavity.

The Pelagiellidae were Lower and Middle Cambrian experiments which underwent a limited radiation, but, as inferred from their tangential aperture, never advanced beyond a mobile browsing form. In contrast, the Onychochilidae, which first appears in the Upper Cambrian, and are inferred from their shell to be mobile browsers, not only persisted in that form but had radiations into two other niches as well. In one major alteration of the basic body plan, the Macluritidae rested their shell on the right side and took up a sedentary mode of life as suspension feeders (Linsley, 1978b). This proved a very successful adaptation and the family is very abundantly represented in Ordovician rocks.

If this group was ancestral to the Euomphalacea as suggested in the "Treatise" (Knight *et al.*, 1960), then this filter feeding adaptation persisted throughout the Paleozoic and was represented in almost every quiet water habitat.

The second major adaptation is assumed by the Clisospiridae and it is one that we do not fully understand. The group includes both low-spired forms like *Clisospira* and *Ferrogyra* as well as high-spired genera like *Atracura, Mimospira,* and *Antizyga.* The low-spired group has a frilled extension around the base and is obviously adapted to holding the shell with the coiling axis highly inclined to the substrate and the base pressed against the substrate. It should be noted that while the macluritids rest their right side on the substrate so that the "spire" is down, the Clisospirids rest their left side against the substrate so that their "spire" is up. As such they are reminiscent of the Pseudophoridae and may have made comparable adaptations (Linsley, Yochelson & Rohr, 1978). The high-spired group is quite puzzling, however, for living gastropods of comparable spire height are all shell draggers, allowing their shell to rest on the substrate behind the cephalopodal mass during locomotion. Yet the highly prosocline aperture and excavated base of the high-spired clisospirids suggests that the shells of these animals were positioned directly over the animal's back so that the axis of coiling is highly inclined relative to the substrate. This would present the organism with a very highly-placed center of gravity which would likely preclude much movement (Linsley, 1978b). It would also be a disadvantageous shell form in an area of any appreciable currents. Possibly, like the Macluritidae, the Clisospiridae were suspension feeders.

TAXONOMIC IMPLICATIONS

The major conclusion of this study is that some groups of Paleozoic shells belong to animals that have not undergone torsion. These groups include the orthostrophic pelagiellids, and the hyperstrophic macluritids, onychochilids, and clisospirids. The euomphalids are included in the discussion because of their resemblance to the macluritids. However, this resemblance may be one of convergence of two very disparate groups rather than phyletic affinity.

The next problem is to determine the sig-

nificance of a group of asymmetrical untorted molluscs. We could: (1) re-define the concept of Gastropoda to accommodate these organisms; (2) we could also re-define the class Monoplacophora for a similar purpose; or (3) we could erect a new class for this strange group.

While there is no single approach which will please every taxonomist, it is our conclusion that these animals should be accommodated in a new class. This conclusion is dictated by the two-fold consideration of our concept of the mechanism of evolution and the significance of the concept of "class." We are quite convinced that evolution proceeded in a mosaic fashion as suggested by Valentine (1979). This model suggests that it was relatively easier to achieve a class rank distinction in the early Paleozoic and progressively more difficult to do so.

One determinant of class rank would be the successful invasion of a new ecological sphere (Valentine, 1979). In the Lower Paleozoic this would be relatively easy since the major habitats were either unoccupied or occupied by organisms with relatively modest adaptive capabilities that offered relatively low-level competition. Thus new classes appear abundantly in the Lower Paleozoic, but with time and perfected adaptations the introduction of a new class becomes progressively more difficult and consequently less frequent.

We envision the early evolution of the Mollusca (the Lower and Middle Cambrian) as experiments taking place in an essentially predator-free sea. As such, the shell served primarily as protection from environmental factors rather than an anti-predation device. In this environment we see two major adaptations (classes) having taken place: the epifaunal molluscs (Monoplacophora) and the infaunal molluscs which have brought the shell down around their gills to protect them from fouling during burrowing (Rostroconcha). In addition there are a number of forms (helcionellids and yochelcionellids) that make no sense as either rostroconchs or monoplacophorans and probably should be accorded class rank. But until we understand the adaptive significance of their shell form and their mode of life, this would seem unwise.

The Upper Cambrian is marked by the advent of predation as produced by the introduction of cephalopods and possibly fish and even some gastropods. The Monoplacophora

reflected this circumstance by surviving either as limpet-shaped forms with presumed low mobility or multiple-whorled, isostrophically coiled forms with a tangential aperture (such as *Cyrtolites*). The latter forms would presumably have greater mobility (Linsley, 1978b). Both of these forms would be restricted to rocky substrates where they could gain protection by clamping. In contrast the Paragastropoda (Onychochilida) and Gastropoda affected deep withdrawal into the shell and were not dependent on clamping against a firm substrate for protection. They were thus able to move out onto sediments. Eventually both presumably evolved opercula to augment the protection afforded by deep withdrawal into their shells. We presume that the gastropods with an anteriorly located aperture and orthostrophic or isostrophic shell were eventually to prove better adapted to this mode of life of browsing on soft sediments. The Paragastropoda, with their posteriorly located apertures and hyperstrophic shells survived only by moving into still another niche, that of essentially sessile, epifaunal suspension feeders. One group, the clisospirids came to rest on their left side while the macluritids came to rest on their right side. The euomphalids resemble the macluritids in their shell form and presumed life-mode and if they are descended from the macluritids then the major successful adaptation of the Paragastropoda was as epifaunal suspension feeders. It is because the Paragastropoda occupy a very different niche from the ancestral Monoplacophora that we feel that they deserve recognition as a new class of the phylum Mollusca rather than aberrant Gastropoda or Monoplacophora.

SYSTEMATIC PALEONTOLOGY
Phylum MOLLUSCA Cuvier, 1797
Class PARAGASTROPODA Linsley & Kier,
new class

Diagnosis—Anisostrophically coiled, untorted mollusks. Shells either hyperstrophic or orthostrophic. Members with elongate apertures with these elongated at approximately right angles to apertural elongation of torted gastropods. The inhalant water current enters under the spire with the result that the "base" of the shell is frequently concave to accommodate the inhalant stream. Position of anus frequently marked by angulation or re-entrant at the outer part of upper whorl surface of aperture. Pretorsional left gill presumably lost.

Stratigraphic distribution—Low. Camb. - Dev. ?Perm.

Order ORTHOSTROPHINA Linsley & Kier, new order

Diagnosis—Orthostrophic paragastropods with either round or elongated apertures.
Stratigraphic distribution—Low. Camb. - Mid. Camb.

Superfamily Pelagiellacea Knight, 1956

Diagnosis—Characters same as order.
Stratigraphic distribution—Low. Camb. - Mid. Camb.

Family Pelagiellidae Knight, 1956

Diagnosis—Orthostrophic, right-handed paragastropods with an elongated tangential aperture. Inhalant current entering near umbilical area, frequently marked by a sinus. Exhalant current exiting near periphery of shell and marked by angulation or even a selenizone generating sinus. Shell rather flattened on top and arched below.
Stratigraphic distribution—Low. Camb. - Mid. Camb.
Genera included—*Pelagiella* Matthew, 1895; *Cambretina* Horný, 1964; *Costipelagiella* Horný, 1964; *Proeccyliopterus* Kobayashi, 1939.

Family ? Aldanellidae Linsley & Kier, new family

Diagnosis—Orthostrophic, right-handed paragastropods with a round, tangential aperture.

We have not been able to judge whether these shells have a tangential aperture.If they do, then they may well be mollusks because the tangential aperture implies a dorsally situated shell. If they have a radial aperture, then we suspect that they are not mollusks. Since aldanellids have a circular aperture we cannot state definitely that they are untorted, but their geological position would suggest that relating them to the penecontemporaneous pelagiellids is a more reasonable approach than suggesting that they are related to gastropods which do not appear until the Upper Cambrian.
Stratigraphic distribution—Low. Camb.

Genera included—*Aldanella* Vostokova, 1962; *Philoxenella* Vostokova, 1962; *Paraaldanella* Golubev, 1976; *Barskovia* Golubev, 1976.

Order HYPERSTROPHINA Linsley & Kier, new order

Diagnosis—Paragastropods with hyperstrophic to depressed-orthostrophic shell, commonly with angulation on outer part of upper whorl surface marking the exhalant channel. Inhalant current entering the mantle cavity at or near umbilicus; long axis of aperture converging toward apex of depressed spire; shell wall thick, outer layers calcitic, inner layers thick, aragonitic but not nacreous; operculum heavy, calcareous, paucispiral in *Maclurites* with attachments for two retractor muscles, unknown in other genera; right ctenidium inferred to have been absent.
Stratigraphic distribution—?Mid. Camb., Up. Camb. - Dev., ?Up. Trias.

Superfamily Onychochilacea Koken, 1925

Diagnosis—Hyperstrophic shells with highly prosocline tangential apertures. Shell form varying from high-spired to moderatey low-spired.
Stratigraphic distribution—Up. Camb. - Dev.

Family Onychochilidae Koken, 1925

Diagnosis—The area of the depressed spire gently rounded into umbilical area with only gentle angulation to mark exhalant area.
Stratigraphic distribution—?Mid. Camb., Up. Camb. - Dev.
Genera included—?*Protoscaevogyra* Kobayashi, 1939; *Matherella* Walcott, 1912; *Kobayashiella* Endo, 1937; *Matherellina* Kobayashi, 1933; *Pervertina* Horný, 1964; *Invertospira* Horný, 1964; *Helicotis* Koken, 1925; *Laeogyra* Perner, 1903; *Onychochilus* Lindström, 1884; ?*Sinistracirsa* Cossmann, 1908; *Hyperstrophema* Horný, 1964; *Versispira* Perner, 1903; *Antispira* Perner, 1903.

Family Clisospiridae Miller, 1889

Diagnosis—The area of the depressed spire with sharp ridge on the upper whorl face.
Stratigraphic distribution—Ord. - Dev.

Subfamily Clisospirinae
Miller, 1889

Diagnosis—Low-spired forms with sharp ridge surrounding depressed spire at periphery and extended upwards and outwards as a frill.
Stratigraphic distribution—Ord. - Sil.
Genera included—*Clisospira* Billings, 1865; *Ferrogyra* Horný, 1964.

Subfamily Trochoclisinae
Horný, 1964 (emend.)

Diagnosis—Herein emended to refer to medium-spired conical clisospirids. Sharp angulation located at whorl periphery. Angulation may be extended upwards and outwards as a frill.
Stratigraphic distribution—Sil. - Dev.
Genera included—*Conoclisa* Horný, 1964; *Trochoclisa* Horný, 1964.

Subfamily Atracurinae
Horný, 1964 (emend.)

Diagnosis—Herein emended to refer to high-spired clisospirids. Sharp angulation located in from the periphery.
Stratigraphic distribution—Ord. - Dev.
Genera included—*Mimospira* Koken, 1925; *Antigyra* Horný, 1964; *Antizyga* Horný, 1964; *Atracura* Horný, 1964; *Bodospira* Wängberg-Eriksson, 1979; *Angulospira* Wängberg-Eriksson, 1979; *Tapinogyra* Wängberg-Eriksson, 1979; *Undospira* Wängberg-Eriksson, 1979.

Superfamily Macluritacea
Fischer, 1885

Diagnosis—Rather large, hyperstrophic shells with radial apertures. Aperture rather elongated with angulation at upper surface that is presumed excurrent. Base flattened or gently protruding.
Stratigraphic distribution—Up. Camb. - Ord.

Family Macluritidae
Fischer, 1885

Diagnosis—Same as Superfamily.
Stratigraphic Distribution—Up. Camb. - Ord.
Genera included—*Scaevogyra* Whitfield, 1878; *Palliseria* Wilson, 1924; *Maclurites*

Lesueur, 1818; *Macluritella* Kirk, 1927; *Teiichispira* Yochelson & Jones, 1958.

? Superfamily Euomphalacea
de Koninck, 1881

Diagnosis—Shell mostly discoidal, orthostrophic or hyperstrophic; aperture round, radial, sometimes with angulation on upper whorl face, representing position of exhalant channel. Presumably with a single gill.
Stratigraphic distribution—Ord. - Perm., ?Up. Trias.

Family Euomphalidae
de Koninck, 1881

Diagnosis—Shell mostly discoidal, typically with wide umbilicus; abandoned early part of whorls closed off by septa; disjunct coiling common.
Stratigraphic distribution—Ord. - Perm., ?Up. Trias.
Genera included—*Ophiletina* Ulrich in Ulrich and Scofield, 1897; *Lytospira* Koken, 1896; *Lecanospira* Butts, 1926; *Barnesella* Bridge & Cloud, 1947; *Euomphalopsis* Ulrich & Bridge, 1931; *Ecculiomphalus* Portlock, 1843; *Lesueurilla* Koken, 1898; *Poleumita* Clarke & Ruedemann, 1903; *Centrifugus* Bronn, 1834; *Sinutropis* Perner, 1903; *Straparollus (Straparollus)* de Montfort, 1810; *S. (Euomphalus)* Sowerby, 1814, *S. (Serpulospira)* Cossmann, 1916; *Nevadaspira* Yochelson, 1971; *S. (Amphiscapha)* Knight, 1942; *S. (Leptomphalus)* Yochelson, 1956; *Pleuronotus* Hall, 1879; *Mastigospira* LaRocque, 1949; *Phanerotinus* Sowerby, 1844; *Cylicioscapha* Yochelson, 1956; *Planotectus* Yochelson, 1956; *Discotropis* Yochelson, 1956; *Austerum*, Heidecker, 1959; *Labrocuspis* Heidecker, 1959.

Family Omphalotrochidae
Knight, 1945

Diagnosis—Shell trochiform, with broad sinus in upper part of outer lip and forward protrusion below; narrowly to widely phaneromphalous, aperture radial.
Stratigraphic distribution—Dev. - M. Perm.
Genera included—*Orecopia* Knight, 1945; *Omphalotrochus* Meek, 1864; *Babylonites* Yochelson, 1956; *Diploconula* Yochelson, 1956.

Family Omphalocirridae
Linsley, 1978

Diagnosis—Large, discoidal shells, frequently with circumbilical keel; early whorls filled with septa at maturity; operculum disc-shaped, multispiral. Exhibit sexual dimorphism.

Stratigraphic distribution—?U. Sil., Dev.

Genera included—*Hypomphalocirrus* Linsley, 1978c; *Omphalocirrus* Ryckholt, 1860; *Liomphalus* Chapman, 1916.

Family Oriostomatidae
Wenz, 1938

Diagnosis—Closely coiled shells with radial apertures; with heavy multispiral calcareous operculum; shell with nacreous inner layer.

Stratigraphic distribution—Up. Sil. - L. Dev.

Genera included—*Morphotropis* Perner, 1903; *Beraunia* Knight, 1937; *Oriostoma* Munier-Chalmas, 1876.

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